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The Larvae of the Anthophoridae (Hymenoptera, Apoidea)
Part 2. The Nomadinae

By Jerome G. Rozen, Jr.[1]

The present paper is the second of a series that treats the phylogeny and taxonomy of the larvae belonging to the bee family Anthophoridae. The first (Rozen, 1965a) dealt with the pollen-collecting tribes Eucerini and Centridini of the Anthophorinae. The present study encompasses the following tribes, all of which consist solely of cuckoo bees: Protepeolini, Epeolini, Nomadini, Ammobatini, Holcopasitini, Biastini, and Neolarrini. For reasons presented below, these tribes are believed to represent a monophyletic group, and consequently all are placed in the Nomadinae. It seems likely that the cleptoparasitic tribes Caenoprosopini, Ammobatoidini, Townsendiellini, Epeoloidini, and Osirini are also members of the subfamily, although their larvae have not as yet been collected. Although the interrelationships of the numerous taxa within the Nomadinae need to be re-evaluated, the tribal concepts used by Michener (1944) are employed here. Adjustments in the classifications will certainly have to be made in the future, however, for Michener (1954) has already indicated, for example, that characters of the adults in the Osirini, the Epeolini, and the Nomadini intergrade.

The affinities of the Nomadinae with the other subfamilies of the Anthophoridae will be discussed in the last paper of the series. Because of char-

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acteristics of both adults and larvae, the other parasitic anthophorids (Rhathymini, Ericrocini, and Melectini) are believed to have a separate evolutionary origin from that of the Nomadinae, and consequently they will be treated in a subsequent paper. Although the first-stage larvae of the Eucerini and the Centridini were described in the first paper, those of the parasitic bees are being reserved for a future study dealing with evolutionary convergence in first instars of cuckoo bees.

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I would like to thank the following people for the loan or gift of specimens: Dr. Fred D. Bennett, Commonwealth Institute of Biological Control, Trinidad, the West Indies; Dr. George E. Bohart and Mr. Philip F. Torchio, Entomology Research Division, United States Department of Agriculture, Logan, Utah; Dr. Earle A. Cross, Jr., Northwestern State College, Natchitoches, Louisiana; Dr. Paul D. Hurd, Jr., University of California, Berkeley; and Dr. Charles D. Michener, the University of Kansas, Lawrence. An expression of appreciation is also due to a number of workers who kindly identified the adult bees that were associated with the larvae; their names are given elsewhere in the paper.

The manuscript was carefully typed and edited by Mrs. Rose Ismay, and my wife, Mrs. Barbara L. Rozen, prepared some of the figures.

NOMADINAE

The Nomadinae are a diverse group and, with such exceptions as *Nomada* and *Triepeolus,* the genera usually contain relatively few species. Although many of the genera tend to be host-specific on a single genus or on only a few genera, the subfamily as a group is successful in that it contains more species and parasitizes a wider range of hosts than any other group of cleptoparasitic bees. The spectrum of hosts includes the Colletidae, Oxaeidae, Halictidae, Andrenidae, Melittidae, and Anthophoridae.

Description of the Nomadinae Based on the Mature Larvae

Head: Integument with or without scattered sensilla; dorsal surface of labrum non-spiculate; epipharynx, hypopharynx, maxillae, and labium spiculate or non-spiculate; mandibles lightly to moderately pigmented. Tentorium complete or incomplete, but in either case with elements extremely slender; only *Isepeolus* with tentorial arms even moderately developed; except in *Isepeolus,* tentorial pits small; posterior pits of *Holcopasites* absent; location of posterior pits in relation to posterior

margin of head and to hypostomal ridge variable; in *Oreopasites* pit anterior to posterior margin and below ridge; in *Neolarra* pit anterior to posterior margin but ridge absent; in *Isepeolus, Nomada,* and *Neopasites* pit anterior to posterior margin and usually on ridge; in most epeolines location of pit difficult to determine because posterior thickening of head capsule and hypostomal ridge poorly defined; posterior thickening of head capsule very weak to virtually absent; hypostomal ridge moderately well developed to absent; pleurostomal ridge moderately developed to absent; epistomal ridge entirely absent to moderately developed laterad of pits and with short extensions mesiad of pits; longitudinal thickening of head capsule absent; vertex projecting slightly or not at all above each antenna. Antennal prominences very low to absent; each papilla shorter than its basal diameter and bearing variable number of sensilla. Labrum protruding variable amount or recessed, with two small to moderate-sized tubercles or, in *Isepeolus,* with single median tubercle; labral apex rounded. Mandible short (except in *Isepeolus*), not massive, and broad to very broad at base, tapering apically to simple point; cusp produced or not, but, if produced, invariably rounded when viewed from above or below, so that apical concavity not sharply defined. Maxillae recessed and broadly fused with labium except in *Isepeolus* in which maxillae and labium are somewhat more separated; maxillary apex rounded or, in *Isepeolus,* subtruncate; apex non-spiculate; galea absent; palpus absent, short, or, in *Isepeolus,* elongate; sclerotized cardo and stipes absent except in *Isepeolus.* Hypopharynx protuberant or recessed. Labium recessed, not divided into prementum and postmentum, and bearing inconspicuous, non-labiate, elongate-oval salivary opening; *Isepeolus* unique in that labium divided, strongly projecting, and bearing conspicuous, labiate, slitlike salivary opening; labial palpi nearly or actually obsolete, except in *Isepeolus* in which palpi are several times longer than basal diameter and equal in length to maxillary palpi.

Body: Form moderately slender to robust and usually gradually tapering anteriorly and posteriorly; each segment not visibly divided dorsally by intrasegmental line except for *Nomada* species C, *Neopasites,* and epeolines in which faint intrasegmental lines are evident and perhaps for *Isepeolus* (see description); either dorsal tubercles absent or each segment projecting slightly dorsolaterally; distinct dorsal and lateral tubercles present only in *Isepeolus.* Integument without setae but in some cases with spicules; dorsal sclerites absent. Spiracles large to small; atrium with or without denticles or spines; atrium usually projecting above body wall, in some cases strongly so; peritreme conspicuous; primary tracheal opening with or without collar; subatrium not divided. Tenth

abdominal segment variously modified; anus situated apically.

Although the Nomadinae, as represented by the larvae described here, are in some respects a diverse group, they share many features. All, with the exception of *Isepeolus viperinus* which is discussed below, have very thin tentorial structures, and the pleurostomal, hypostomal, and even epistomal ridges tend to be reduced. There is also a marked trend for the posterior thickening of the head capsule to be faint or even obliterated. The peculiar positions of the posterior tentorial pits are almost without precedent among the Apoidea, and the absence of antennal prominences and the non-protuberant vertex impart a distinctive aspect to the head. Perhaps the most important feature signifying a close interrelationship is the tapering, apically pointed, and simple mandible shared by all known larvae. With the exception of *Isepeolus* and to a lesser extent *Neopasites* and *Neolarra,* the other mouth parts are remarkably similar—protuberant hypopharynx, recessed maxillae and labium, short maxillary palpi, nearly non-existent labial palpi, and small, non-labiate salivary opening. With the exception of *Isepeolus,* the postcephalic region of nomadine larvae exhibits marked homogeneity, especially in the streamlined shape of the body, the absence of dorsal tubercles, and the apically situated anus.

It might be argued that these features have evolved separately in connection with multiple origins of cleptoparasitism in the Anthophoridae. After all, the long-mandibled, first-larval instar found in many unrelated groups of parasitic apoids is a good example of convergent evolution in regard to cleptoparasitism. Although such possibilities must be considered, I believe the evidence substantiates without question a monophyletic origin for most of the elements in the subfamily. First, the similarities (listed above) of these larvae are too great and too numerous to make convergent evolution a likely hypothesis. Second, cleptoparasitism has arisen elsewhere in the Anthophoridae, namely, in the Ericrocini, Melectini, and Rhathymini. Although the larval representatives of these groups have not been studied in detail, a brief examination clearly indicates that they are amply distinct from those of the Nomadinae. This fact demonstrates that cleptoparasitism in the anthophorids does not have as a requisite a single rigid set of adaptive anatomical features and therefore suggests that the similarities of the Nomadinae result from common descent rather than convergence.

Neolarra and *Neopasites,* as indicated above, are somewhat aberrant in that the labium projects as far as or farther than the hypopharynx and that the frontoclypeal region is somewhat protuberant. In all other important features they agree with the other Nomadinae and we can safely

assume that they arose from nomadine stock but have perhaps diverged somewhat farther than other groups.

Only the relationship of *Isepeolus* with the nomadines remains somewhat in doubt. It has been included here with the other nomadines because of the forward position of the posterior tentorial pits, the weak posterior thickening of the head capsule, the reduced pleurostomal ridge, the reduced vertex, the shape of the mandible, and the possibly intermediate condition of the labroclypeal region of *Epeolus pusillus*. In other respects the mature larva is quite unlike that of the Nomadinae, as follows: tentorium more strongly developed; posterior tentorial pits conspicuous; single median labral tubercle present; mandible elongate; labiomaxillary region and associated features adapted for cocoon production; and body with both dorsolateral and lateral tubercles. As discussed below, these features are here interpreted as signifying that *Isepeolus* is an early offshoot of the ancestral nomadine stock. However, they might also indicate that *Isepeolus* arose from quite another lineage and developed the nomadine-like characters *de novo*. Perhaps the larvae of other Protepeolini, when found, will bring additional evidence to bear on the problem.

The Interrelationships of the Nomadinae

The following analysis of the evolutionary relationships within the Nomadinae is based solely on the larvae treated in this paper. Because so few taxa are represented, this analysis is obviously tentative. I present it here as a hypothesis with the hope that it will stimulate a critical review of nomadine phylogeny based on all available lines of evidence.

In the present study major characters of taxonomic importance are evaluated as primitive (plesiomorphic) or derived (apomorphic). If a feature of a nomadine is found generally among the larvae of bees, it is judged primitive. Consequently a modification of this feature within the Nomadinae is considered a derived characteristic. For example, the well-developed tentorial structures found in *Isepeolus* are characteristic of almost all bee larvae. It seems probable, therefore, that they are a primitive feature and that the very thin tentorial arms of others of the Nomadinae represent an apomorphic feature derived from the *Isepeolus*-like tentorium. Some features seem to be further modifications of derived characters. For example, the lost maxillary palpi of *Neolarra* and *Neopasites* are a condition probably preceded by a reduction in palpal size such as is found in the epeolines. Also, a character may change in various ways in different organisms during the course of evolution. Hence, the enlarged labrum of *Nomada* and the much-reduced labrum of *Neolarra*

and *Neopasites* are both modifications of the normal type of labrum.

The primitive features of the Nomadinae are as follows: tentorium well developed; posterior margin of head capsule with a single transverse line; hypostomal ridge well developed; labrum exceeding frontal region when larva seen in lateral view; paired labral tubercles; maxillary palpi elongate; labium protruding and divided into prementum and postmentum[1]; labium non-spiculate, exceeding hypopharynx, and with elongate palpi; most body segments with lateral tubercles; ninth abdominal segment normal; tenth abdominal segment normal.

When the analysis was begun, not all features used in taxonomic discrimination could be evaluated in terms of primitive or derived. For example, it could not be said with any degree of certainty whether a spiculated hypopharynx is derived from a non-spiculated hypopharynx, or vice versa, as both conditions are found widely among bee larvae. However, after the phylogeny of the Nomadinae was charted (fig. 1), most of these indeterminate characters could be classified, with the result that the following are also believed primitive: hypopharynx spiculate; maxillae non-spiculate; spiracular atrium without spines and atrium projecting above the body wall.

The characters listed in the preceding two paragraphs, then, are presumed to be the features of the cleptoparasitic ancestral lineage (fig. 1, 1) that gave rise to the present Nomadinae. *Isepeolus* possesses most of these features. However, the *Isepeolus* line (fig. 1, 2) developed a single, median, labral tubercle in place of the paired labral tubercles, the body developed lateral tubercles, and the tenth segment became short. It is unknown whether the dorsolateral body tubercles of *Isepeolus* are a characteristic of the ancestral type of the Nomadinae or whether they evolved at the same time as the lateral body tubercles.

The original ancestral lineage evolved into another line (fig. 1, 3) with the following apomorphic characteristics: tentorium reduced; hypostomal ridge weak; maxillary palpi short; labium recessed and not divided into prementum and postmentum; labial palpi lost or almost lost; and

[1] The various modifications (produced labial region, elongate palpi, and others) associated with cocoon spinning are believed to be primitive. It might be argued that because features (reduced labial region, short palpi, and others) associated with the non-cocoon-spinning habit are widely found among other bees, they should be considered primitive instead. However, the salivary opening of the non-cocoon-spinning nomadines is quite unlike that of the panurgines, andrenines, and halictines, all of which are non-cocoon spinning. The suggestion is that the non-cocoon-spinning habit and correlated anatomical features are an independent evolutionary development in the Nomadinae and were preceded by the cocoon-spinning habit.

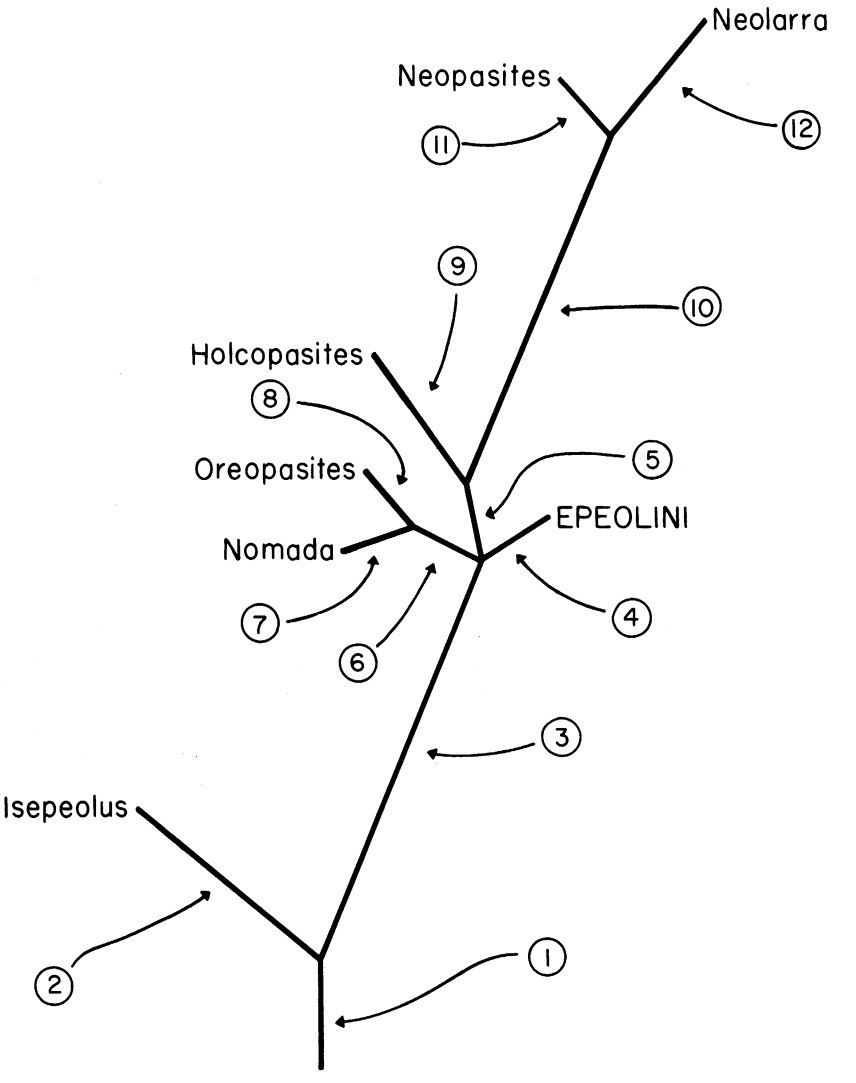


FIG. 1. Phylogenetic diagram of the Nomadinae based on the mature larvae. For explanation of numbers see text. Length of lines indicates in a general way the degree of anatomical change. The directions of the lines and the angles have no meaning.

hypopharynx exceeding labium. This was the main nomadine evolutionary line: One offshoot (fig. 1, 4) gave rise to the Epeolini with the large

atrial spines. Another offshoot (fig. 1, 6) changed to a form with two transverse lines at the posterior margin of the head. This offshoot then branched, one limb (fig. 1, 8) leading to *Oreopasites* with its non-spiculate hypopharynx, and the other (fig. 1, 7), to *Nomada* with its enlarged labrum. The third offshoot (fig. 1, 5) of the main evolutionary line developed into the rest of the taxa, all characterized by the loss or near loss of projecting maxillary palpi. The *Holcopasites* lineage (fig. 1, 9) branched from this offshoot, lost the posterior tentorial arms, and developed a spiculated produced venter to the tenth abdominal segment. The third offshoot (fig. 1, 10), after giving rise to the ancestor of *Holcopasites,* underwent considerable modification resulting in the following characteristics: frontal clypeal area overhanging labrum; maxillae spiculate; labium projecting somewhat beyond hypopharynx; hypopharynx non-spiculate; and ninth segment elongate ventrally. The lineage then split; one limb (fig. 1, 11) led to *Neopasites* with its short terminal body segment, and the other (fig. 1, 12), to *Neolarra* with its spiculate labium and elongate tenth segment.

It should be stressed that in the development of the diagram (fig. 1) an attempt was made to postulate as few multiple origins of a feature as possible. However, the analysis indicates that the shortened tenth abdominal segment evolved twice—once in *Isepeolus* and once in *Neopasites.* Further, the non-spiculate condition of the hypopharynx presumably had a separate evolutionary origin in *Oreopasites* and in the lineage leading to *Neolarra* and *Neopasites.* Lastly, the spiculate maxillae apparently evolved separately in *Odyneropsis* of the epeolines and in the *Neolarra-Neopasites* lineage. As all these features are found here and there throughout the larvae of the Apoidea, they cannot be considered stable evolutionary characters, and therefore their multiple origin within the Nomadinae seems plausible. Although the labium of *Isepeolus* and the *Neolarra-Neopasites* lineage projects beyond the hypopharynx, the structure of the labia in these two lines is so different that the projections almost certainly are not homologous.

Key to Postdefecating Larvae of the Nomadinae

The larvae of a number of species of both *Oreopasites* and *Triepeolus* exhibit very little interspecific variation. For this reason the following key, though based on few species, may be useful for the identification of postdefecating nomadine larvae to genus.

1. Lateral body tubercles (fig. 2) present; labium (figs. 4, 5) strongly projecting and bearing conspicuous, transverse salivary lips; labial palpus (fig. 5) several times longer than basal diameter; labrum (figs. 4, 5) with single median tubercle.....

. . . . . *Isepeolus viperinus* (Holmberg)

Lateral body tubercles (figs. 8, 41) absent; labiomaxillary region (figs. 39, 40) recessed and salivary opening inconspicuous and elongate-oval; labial palpus (fig. 39) absent or only a vague swelling; labrum (figs. 39, 40) with two small to moderate-sized tubercles 2

2(1). Frontoclypeal region overhanging recessed labrum as seen in lateral view (figs. 75, 82); adoral surface of mandible much shorter than outer surface when mandible (fig. 78) viewed from above or below 3

Frontoclypeal region (figs. 39, 40) not protruding so far as labrum which is not recessed; mandible with adoral surface at least nearly as long as outer surface (fig. 56) 4

3(2). Tenth abdominal segment elongate (fig. 79); labium spiculate apically (figs. 81, 82) . . . . . *Neolarra pruinosa* Ashmead

Tenth abdominal segment short (fig. 72); labium non-spiculate (figs. 74, 76) . . . . . *Neopasites cressoni* Cockerell

4(2). Spiracular atria (figs. 11, 23, 35) beset with numerous elongate spines; spiracles (figs. 8, 24) large 5

Spiracular atria smooth or with small denticles (figs. 46, 63); spiracles (figs. 41, 59) normal in size 7

5(4). Mandibular apex (figs. 36–38) produced into long tooth; maxillae (fig. 34) spiculate . . . . . *Odyneropsis apicalis* Ducke

Mandibular apex (figs. 12–14) normal; maxillae (fig. 10) non-spiculate 6

6(5). Mandible, as seen in adoral view (fig. 31), tapering gradually toward apex . . . . . *Epeolus* species A

Epeolus pusillus Cresson

Mandible, as seen in adoral view (figs. 13, 18, 21) narrowing abruptly so that apical section nearly parallel-sided . . . . . *Triepeolus* species A

Triepeolus species B

Triepeolus species C

Triepeolus mesillae Cockerell

Triepeolus remigatus (Fabricius)

7(4). Tenth abdominal segment (fig. 69) produced ventrally and bearing patch of darkly pigmented spicules medially . . . *Holcopasites insoletus* (Linsley)?

Holcopasites species A

Holcopasites calliopsidis (Linsley)

Tenth abdominal segment (fig. 41) not produced ventrally (or in *Nomada* species B, fig. 50, only slightly produced posteroventrally) and not bearing spicules 8

8(7). Hypopharynx (figs. 39, 40) spiculate; integument of postdefecating larva smooth and shiny; labrum (figs. 40, 53) more or less abnormally protuberant . . . . . *Nomada,* 9

Hypopharynx (Rozen, 1954, figs. 5, 6) non-spiculate; integument of postdefecating larva wrinkled; labrum normal . . . . . *Oreopasites vanduzeei* Cockerell

9(8). Labrum with pronounced, sharp-pointed spicules apically; mandibular cusp non-dentate (figs. 43, 44) . . . . . *Nomada* species A

Labrum non-spiculate apically (figs. 39, 40); mandibular cusp more or

less dentate (figs. 49, 51) 10
10(9). Antennal papillae longer (fig. 48) ..... *Nomada suavis* Cresson
Antennal papillae shorter (fig. 40) ..... *Nomada fowleri* Cockerell
Nomada species B

TRIBE PROTEPEOLINI

This is a small group containing two or three genera. The larva of only *Isepeolus* is known.

ISEPEOLUS COCKERELL

Claude-Joseph (1926) briefly described and illustrated the mature larva of *Isepeolus luctuosus* (Spinola). Although Michener (1957) treated the first instar of *I. viperinus,* the following is the first report of the mature form. The larvae of these two species appear to be quite similar.

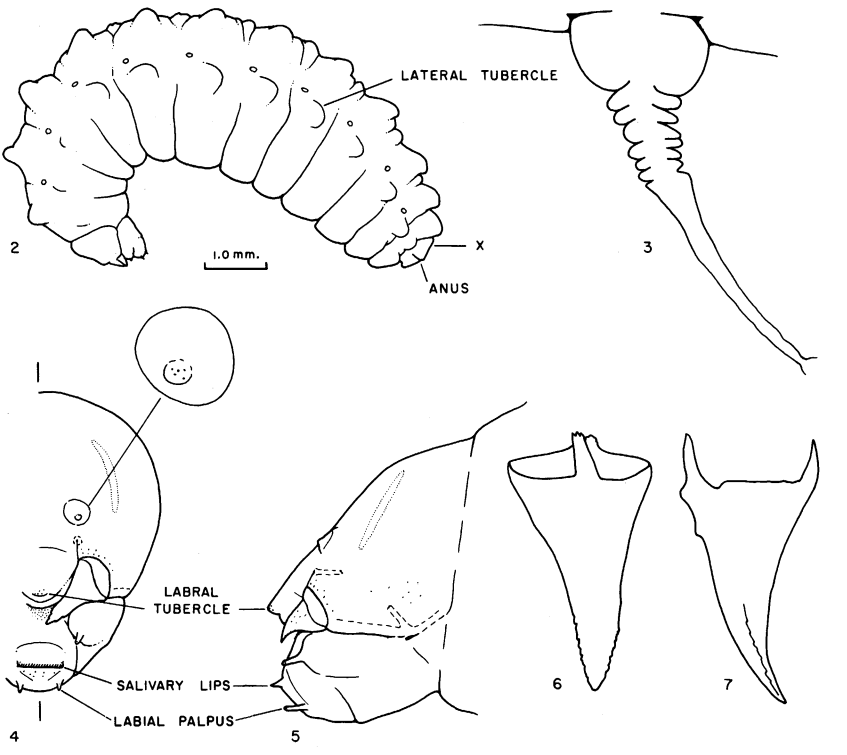
Isepeolus viperinus (Holmberg)

Figures 2–7

Total length, 8.0 mm.

HEAD (FIGS. 4, 5): Integument lightly sclerotized and unpigmented except for apex of mandibles; scattered sensilla present; hypopharynx spiculate; epipharynx, maxillae, and labium non-spiculate. Tentorium complete; anterior arms moderately thick; pits well developed; dorsal arms thin but present; posterior arms perhaps somewhat thinner than anterior arms and arising from posterior end of hypostomal ridge or from just below it; posterior pits conspicuous, situated anterior to posterior margin of head; tentorial bridge thin; posterior thickening of head capsule very weak except as it bends forward near posterior tentorial pits where it appears to be posterior extension of hypostomal ridge; hypostomal ridge well developed; pleurostomal ridge scarcely visible; epistomal ridge absent between anterior tentorial pits and scarcely visible laterad (or below) pits; cleavage lines absent; parietal bands moderately faint. Antennal papillae low, each bearing four or five sensilla. Labrum exceeding frontal region and bearing single median tubercle[1]; epipharynx without basal lobelike swelling. Mandible (figs. 6, 7) tapering apically to broad point; upper and lower apical edges finely serrate;

[1] This tubercle may not be a homologue of the labral tubercles of the other larvae treated here. In addition to labral tubercles, the Epeolini, especially *Epeolus,* have a median cluster of sensilla near the base of the labrum. In *Epeolus pusillus* this cluster is on a swelling that is suggestive of, though less pronounced than, the median tubercle of *Isepeolus.* If the swelling in *Epeolus pusillus* and the tubercle of *Isepeolus* are homologous, then it is to be assumed that the true labral tubercles of *Isepeolus* have been lost.



FIGS. 2–7. Postdefecating larva of *Isepeolus viperinus* (Holmberg). 2. Entire larva, lateral view. 3. Spiracle. 4. Head capsule, frontal view. 5. Same, lateral view. 6, 7. Left mandible, inner and ventral views.
Scale refers to figure 2.

cusp not produced and not dentate. Maxillae moderately broadly fused to labium; palpi elongate; cardo and stipes (unlike those of other nomadines) somewhat sclerotic. Labium projecting, divided into prementum and postmentum; palpi well developed, similar in length to those of maxillae. Hypopharynx exceeded by labium. Salivary opening an elongate transverse slit on strongly projecting lips.

BODY: General shape of postdefecating larva (fig. 2) not similar to that of other nomadine larvae; form moderately robust, slightly curved; each body segment divided dorsally by several transverse creases (the dorsal subdivisions of each body segment may not be homologous with the cephalic and caudal annulations of the pollen-collecting anthophorids because of the extreme narrowness of the anterior annulation in this

specimen; unfortunately the rather poor condition of the specimen prohibited a study of its musculature, for the intrasegmental line can be identified by its association with the oblique muscles); dorsolateral tubercles conical (that is, not transverse), well developed though not strongly projecting; lateral tubercles well developed, being similar to dorsal tubercles. Integument non-setose, non-spiculate, finely wrinkled and dull. Spiracles (fig. 3) moderate in size, not on sclerites; atrium projecting above body wall, with rim; atrial wall smooth; peritreme flat; primary tracheal opening with collar. Ninth abdominal segment normal; tenth segment short; without spicules, and otherwise apparently unmodified.

MATERIAL STUDIED: One postdefecating larva, Curitiba, Brazil, January 15, 1956, from nest of *Colletes kerri* Moure (C. D. Michener), in the collection of the University of Kansas. Michener (1957) reported on the biology of this species and described its first-stage larva.

TRIBE EPEOLINI

The mature larvae of the three genera represented here are similar and can be separated from those of others of the Nomadinae on the basis of various characteristics of the spiracles.

TRIEPEOLUS ROBERTSON

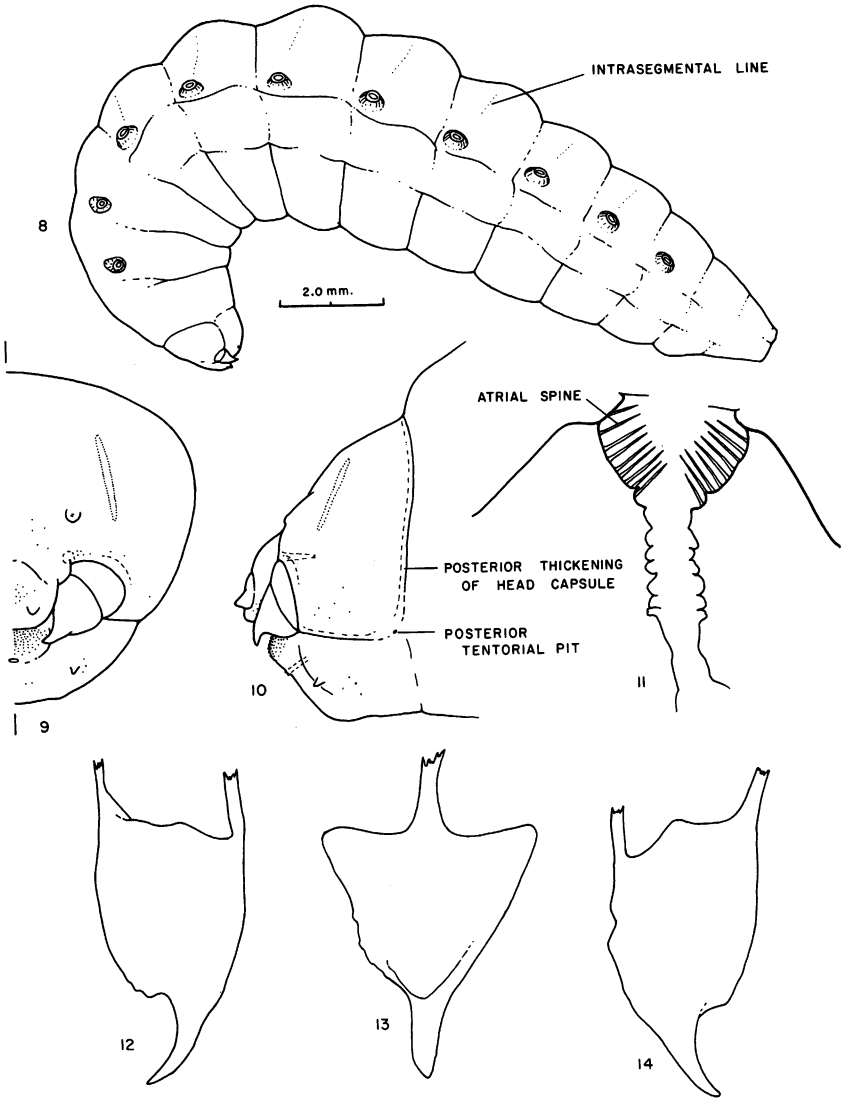
Although only two species have been identified, the five lots treated here come from widely separated areas and are parasites of different genera (and even families) of hosts. These facts, supported by anatomical differences, indicate that five distinct species are represented; all resemble one another closely.

Triepeolus Species A

Figures 8–14

Total length, 14.5–17.0 mm.

HEAD (FIGS. 9, 10): Integument, including mandibular corium, darkly pigmented; scattered sensilla present; hypopharynx spiculate; epipharynx spiculate laterally; maxillae and labium non-spiculate. Tentorium complete, but arms extremely slender; both anterior and posterior pits small; position of posterior pit in relationship to ridge difficult to determine, but pit anterior to posterior margin of head; posterior thickening of head capsule very weak; hypostomal ridge very weak but pigmented except in area of posterior pit; pleurostomal ridge very weak but more darkly pigmented than surrounding cuticle; because anterior tentorial pits lie next to anterior mandibular articulations, epistomal ridge laterad of pits



FIGS. 8–14. Postdefecating larva of *Triepeolus* species A. 8. Live larva, lateral view. 9. Head capsule, frontal view. 10. Same, lateral view. 11. Spiracle. 12–14. Left mandible, dorsal, inner, and ventral views.

Scale refers to figure 8.

cannot be distinguished from tentorium; ridge absent mesiad of pits; coronal cleavage line evident as a light line extending anteriorly to clypeal region; parietal bands moderately expressed. Antennal papillae low, each bearing perhaps four closely grouped sensilla. Labrum a protruding lobe bearing two moderate-sized tubercles; epipharynx without basal lobelike swelling. Mandible (figs. 12–14) very stout at base and slender apically; upper and lower apical edges not truly serrate but with few irregular minute projections; cusp produced but rounded and not dentate. Maxillae broadly fused with labium; palpi small but evident. Labium not divided into prementum and postmentum; palpus lost except perhaps for several sensilla. Hypopharynx exceeding maxillae and labium. Salivary opening small, elongate-oval, and surrounded by dark, slightly projecting rim.

BODY: General shape (fig. 8) of postdefecating form moderately robust anteriorly but gradually tapering posteriorly and with anterior end strongly curved; each body segment not conspicuously divided into cephalic and caudal annulets; faint though distinct intrasegmental lines present; dorsal tubercles absent; color distinctly yellow. Integument of postdefecating larva rigid, non-setose, finely wrinkled, dull, and with only limited patch of spicules on ventral surface. Spiracles (fig. 11) large, on projecting, pigmented sclerites; atrium projecting above body wall, with rim; atrial wall beset with numerous long spines; peritreme flat; primary tracheal opening without collar. Ninth abdominal segment normal; tenth segment perhaps somewhat elongate, not produced ventrally, and without spicules.

MATERIAL STUDIED: Six postdefecating larvae, Portal, Cochise County, Arizona, August, 1964, from cells of *Ptiloglossa jonesi* Timberlake (M. A. Cazier and M. Mortenson), in the collection of the American Museum of Natural History.

Triepeolus Species B

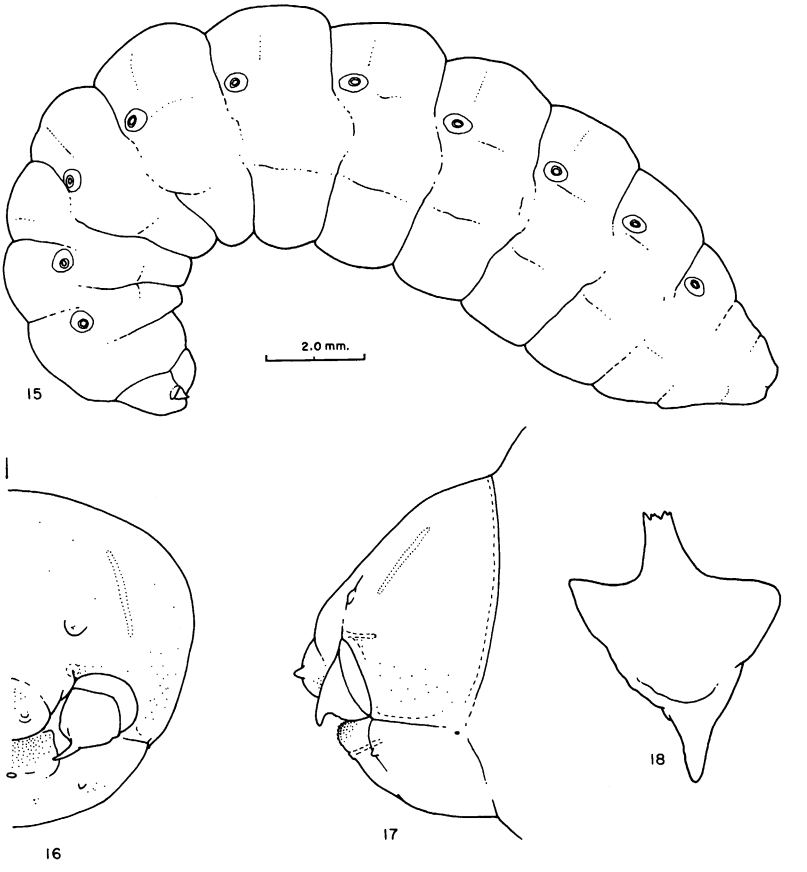
Figures 15–18

Total length, 15.0 mm.

HEAD (FIGS. 16, 17): As in *Triepeolus* species A except for following: scattered setae more numerous; pigmentation of hypostomal ridge and pleurostomal ridge reduced; antennal prominences expressed slightly less; mandible as seen in adoral view (fig. 18) tapering more gradually.

BODY (FIG. 15): As in *Triepeolus* species A except for following: integument non-spiculate; spiracular sclerites lower; tenth abdominal segment slightly shorter.

MATERIAL STUDIED: One postdefecating larva, 1 mile north of Rodeo, Hidalgo County, New Mexico, 1963, from nest of *Protoxaea gloriosa* (Fox) (M. A. Cazier and M. Mortenson), in the collection of the American Museum of Natural History.



FIGS. 15–18. Postdefecating larva of *Triepeolus* species B. 15. Live larva, lateral view. 16. Head capsule, frontal view. 17. Same, lateral view. 18. Mandible, inner view.

Scale refers to figure 15.

Triepeolus Species C

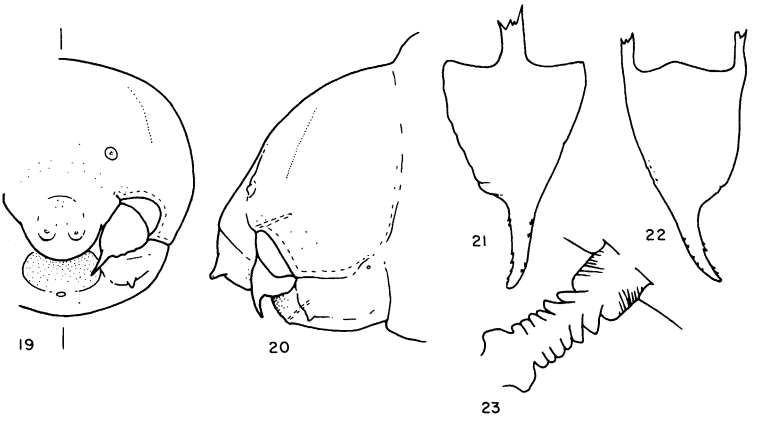
The specimens treated here are the same as those studied by Michener (1953) as *Triepeolus* sp. ? Although Michener thoroughly described and

illustrated them, the following account is given for comparison with the other species.

Total length, 11.0–12.0 mm.

HEAD: As described for *Triepeolus* species A except for following: mandibular cusp much less produced (see Michener, 1953, fig. 194); position of posterior tentorial pit in relation to hypostomal ridge not so well defined as illustrated by Michener (1953, fig. 191) nor are labial palpi evident (*ibid.*, figs. 191, 192).

BODY: As described for *Triepeolus* species A except for following: integu-



FIGS. 19–23. Postdefecating larva of *Triepeolus mesillae* Cockerell. 19. Head capsule, frontal view. 20. Same, lateral view. 21, 22. Mandible, inner and ventral views. 23. Spiracle.

ment non-spiculate; spiracular sclerites not so prominent; tenth abdominal segment shorter, more like that of *Triepeolus* species B.

The outer portion of the atrium does not seem to slope in, as indicated by Michener, but appears very similar to that of *Triepeolus* species A.

MATERIAL STUDIED: Seven postdefecating larvae, Marsh Creek Canyon, Contra Costa County, California, February 18, 1947, on *Melissodes* sp. (J. W. MacSwain and G. E. Bohart), in the collection of the California Insect Survey.

Triepeolus mesillae Cockerell

Figures 19–23

Total length, 8.0 mm.

HEAD (FIGS. 19, 20): As described for *Triepeolus* species A except for following: although pigmentation of head capsule of postdefecating form

as described for *Triepeolus* species A, that of predefecating form only very faintly pigmented except for dark hypostomal and pleurostomal ridges; posterior tentorial pit below hypostomal ridge; antennal papillae with six sensilla on one side and seven on other; upper and lower mandibular margins (figs. 21, 22) with distinct teeth; projecting rim on salivary opening not dark in predefecating larva.

BODY: Specimens poorly preserved so that shape of body and some features of postcephalic region not definitely known; color of postdefecating form yellow, that of predefecating form whitish. Integument nonsetose, spiculate in some areas; integument of postdefecating larva rigid, finely wrinkled and dull, that of predefecating form not rigid. Spiracles (fig. 23) as described for *Triepeolus* species A except primary tracheal opening with collar and projecting pigmented sclerites not very evident on predefecating larva. Tip of abdomen apparently as described for *Triepeolus* species A.

MATERIAL STUDIED: One predefecating larva, Lakeview, Douglas County, Kansas, September 11, 1955, parasite of *Nomia triangulifera* Vachal (E. A. Cross); one postdefecating larva, same, except April 11, 1955; both in the collection of the University of Kansas. Associated adults identified by Paul D. Hurd, Jr.

Triepeolus remigatus (Fabricius)

Figure 24

Total length, 13.0 mm.

HEAD: As described for *Triepeolus* species A except for following: in contrast to postdefecating larva, head capsule of predefecating larva lightly pigmented, mandibles darkly pigmented, all other areas including mandibular corium unpigmented; pleurostomal and hypostomal ridges of postdefecating form not so darkly pigmented as those of *Triepeolus* species A; light coronal cleavage line not extending so far forward; anterior portion of line replaced by slight external ridge; mandibular apex tapering more gradually like that of *Triepeolus* species B.

BODY: General shape and integument of postdefecating form as in *Triepeolus* species A except integument non-spiculate; predefecating larva (fig. 24) moderately robust, without tapering aspect to abdomen as found in postdefecating form; although specimen poorly preserved, intrasegmental lines of predefecating form apparently not evident; color of predefecating form much paler than that of postdefecating form. Spiracles as in *Triepeolus* species A except those of predefecating form not on elevated, pigmented sclerites. Ninth and tenth abdominal segments as in *Triepeolus* species A except perhaps somewhat shorter.

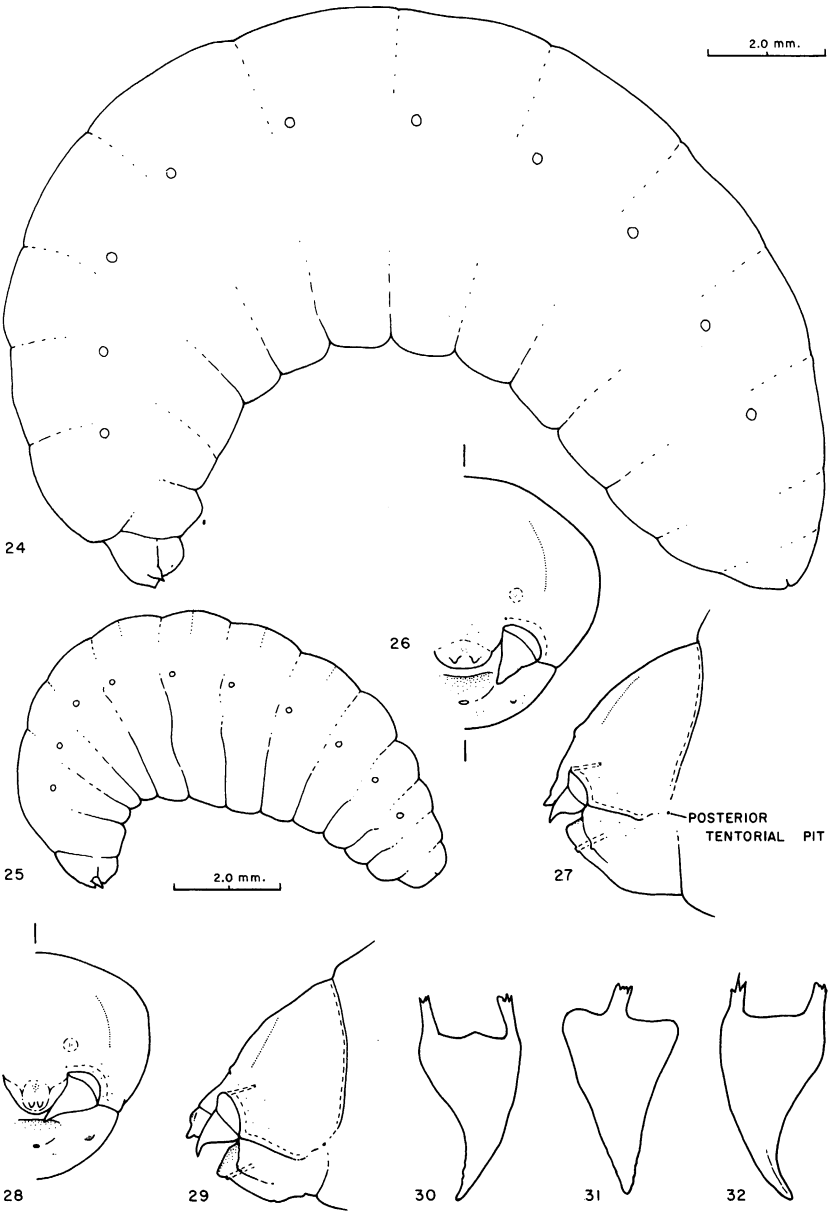


FIG. 24. Predefecating larva of *Triepeolus remigatus* (Fabricius), lateral view.

FIGS. 25–27. Postdefecating larva of *Epeolus* species A. 25. Entire larva, lateral view. 26. Head capsule, frontal view. 27. Same, lateral view.

FIGS. 28–32. Mature larva of *Epeolus pusillus* Cresson. 28. Head capsule, frontal view. 29. Same, lateral view. 30–32. Left mandible, dorsal, inner, and ventral views.

Scale refers to figures 24 and 25.

MATERIAL STUDIED: One postdefecating form, one predefecating form, and several earlier stages, Beltsville, Prince Georges County, Maryland, August 1, 1957, from nest of *Xenoglossa strenua* (Cresson) (G. E. Bohart), in the collection of G. E. Bohart. Identified by G. E. Bohart.

EPEOLUS LATREILLE

It is obvious from this study that the larvae of *Triepeolus* and those of this genus agree closely.

Epeolus Species A

Figures 25–27

The following account is based on the same specimens studied by Michener (1953). Although he compared them with *Triepeolus,* additional comparisons are now in order because new characters have come to light.

Total length, 9.0 mm.

HEAD (FIGS. 26, 27): As described for *Triepeolus* species A except for following: integument not so darkly pigmented; hypopharynx less distinctly spiculate; tentorium presumably incomplete, but in any event anterior and posterior arms extremely thin; coronal cleavage line faint; antennal sensilla two to three on each side; apical part of mandible (Michener, 1953, figs. 195, 196) broader; cusp not at all produced; labial palpi perhaps indicated by very small swelling in addition to sensilla.

BODY: Although specimens somewhat poorly preserved, general body shape (fig. 25) similar to that of *Triepeolus* species A; each body segment not conspicuously divided into cephalic and caudal annulets; faint though distinct intrasegmental lines present; dorsal tubercles absent; color yellowish. Integument of postdefecating form non-setose, non-spiculate, finely wrinkled, dull, and presumably rigid. Spiracles large; spiracular sclerites much smaller than in *Triepeolus*; other spiracular features as illustrated by Michener (1953, fig. 198). Ninth and tenth abdominal segments normal in length and perhaps with ventral part of ninth projecting ventrally, unlike that of *Triepeolus.*

MATERIAL STUDIED: Two postdefecating larvae, Bodega Bay, Sonoma County, California, January 14, 1948, on *Colletes fulgidus* Swenk? (J. W. MacSwain), in the collection of the California Insect Survey.

Epeolus pusillus Cresson

Figures 28–32

This species seems to differ from *Epeolus* species A in the peculiar shape

of the labrum and the somewhat more protuberant clypeus. The general appearance of the labioclypeal region is somewhat suggestive of *Isepeolus viperinus,* which also is a parasite of *Colletes.*

Total length, 9.0 mm.

HEAD (FIGS. 28, 29): As described for *Triepeolus* species A except for following: integument not so darkly pigmented; hypopharynx not so distinctly pigmented; coronal cleavage line not evident; labrum narrowed, as seen from in front and somewhat protuberant basally as seen laterally; labral tubercles nearly contiguous, more so even than those of *Epeolus* species A; mandible (figs. 30–32) similar to that of *Epeolus* species A.

BODY: Although specimen poorly preserved, body shape apparently similar to that of *Epeolus* species A. Spiracles as described for *Epeolus* species A, but atrium more strongly projecting. Ninth and tenth abdominal segments as described for *Epeolus* species A.

MATERIAL STUDIED: One postdefecating larva, Myton, Duchesne County, Utah, October, 1962, from cell of *Colletes deserticola* Timberlake (G. E. Bohart), in the collection of G. E. Bohart. Identified by G. E. Bohart.

ODYNEROPSIS SCHROTTKY

Odyneropsis apicalis Ducke

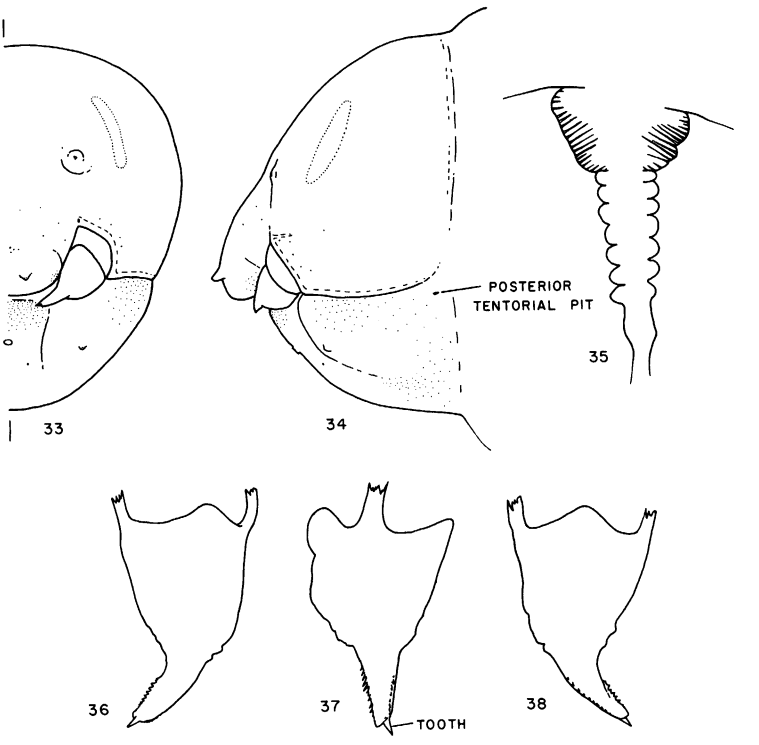
Figures 33–38

Because our knowledge of the larva of this species is based only on the cast skin of the last instar, the description presented here is incomplete, and the outlines of the head capsule illustrated in the figures are reconstructions. However, it is surprising how much information can be obtained from a well-preserved cast skin.

Total length unknown, but undoubtedly more than 10.0 mm.

HEAD (FIGS. 33, 34): Integument lightly pigmented; scattered sensilla present; hypopharynx distinctly but finely spiculate; epipharynx spiculate laterally; maxilla with fine spicules over most of surface; labium nonspiculate. Anterior and posterior tentorial pits fine and connecting arms extremely slender; posterior pits situated well below hypostomal ridge and anterior to posterior margin of head; other features of tentorium not known; posterior thickening of head capsule very weak; hypostomal and pleurostomal ridges rather weak and slender but darkly pigmented and therefore well defined; because anterior tentorial pits lie next to anterior mandibular articulations, epistomal ridge laterad of each pit cannot be identified; ridge absent mesiad of pits; condition of coronal cleavage line not known; parietal bands moderately well expressed. Antennal papillae low, though perhaps somewhat more pronounced than illustrated, and each with six or seven sensilla. Labrum a protruding lobe bearing two

moderately small tubercles; epipharynx without basal lobelike swelling. Mandible (figs. 36–38) very stout at base and moderately slender apically; upper and lower apical edges with distinct teeth; apex produced into elongate tooth adoral to which there is a broad, flat projection; cusp only slightly projecting, non-dentate. Maxillae broadly fused with labium; palpi small but evident. Labium not divided into prementum and post-



FIGS. 33–38. Mature larva of *Odyneropsis apicalis* Ducke drawn from cast skin. 33. Head capsule, frontal view. 34. Same, lateral view. 35. Spiracle. 36–38. Left mandible, dorsal, inner, and ventral views.

mentum; palpus represented only by sensillum. Hypopharynx exceeding maxillae and labium. Salivary opening small, elongate-oval, and surrounded by slightly projecting rim.

BODY: Shape and color not known. Integument of postdefecating form rigid, non-setose, but with some small spicules. Spiracles (fig. 35) large, perhaps on slightly projecting, narrow, lightly pigmented sclerites; atrium not projecting above body wall, without rim; atrial wall with numerous

long spines; peritreme flat; primary tracheal opening without collar. Shape of ninth and tenth abdominal segments not known.

MATERIAL STUDIED: One cast skin of postdefecating larva, Nariva Swamp, Trinidad, the West Indies, March, 1965, from cell of *Ptiloglossa* sp. (F. D. Bennett). Identified by C. D. Michener.

TRIBE NOMADINI

Although a large tribe, most genera of the Nomadini are small and infrequently encountered. Larvae of the large and widely distributed genus *Nomada* are the only ones that have been collected.

NOMADA SCOPOLI

The larvae described below are quite homogeneous.

Nomada (*Nomada*) *fowleri* Cockerell

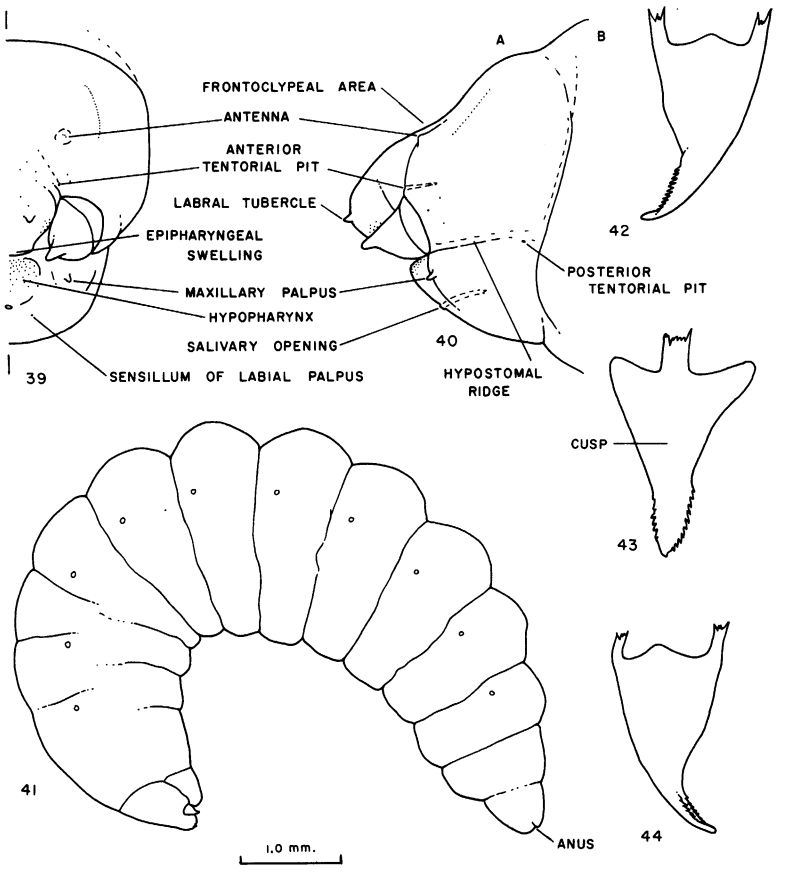
Figures 39, 40

The specimens examined by Michener (1953) are redescribed so that they can be compared with other *Nomada* larvae.

Total length, 7.0 mm.

HEAD (FIGS. 39, 40): Integument lightly pigmented; very few scattered sensilla present; hypopharynx spiculate; epipharynx spiculate only laterally; maxillae and labium non-spiculate. Tentorium extremely thin but apparently complete; both anterior and posterior pits small but present; posterior pit situated considerably anterior to posterior margin of head and perhaps somewhat below hypostomal ridge; posterior thickening of head capsule scarcely evident laterally; head capsule dorsally bounded posteriorly by two faint lines (fig. 40, A and B), one in front of other[1]; hypostomal ridge very weak; pleurostomal ridge virtually absent; epistomal ridge evident laterad of anterior tentorial pits but with only faint extensions running short distance mesiad of pits; cleavage line not visible; parietal bands weakly expressed. Antennal papillae low, each bearing approximately three closely grouped sensilla. Labrum a strongly projecting lobe bearing two small tubercles; epipharynx with lobelike swelling basally, immediately above hypopharynx (fig. 39). Mandible (Michener, 1953, figs. 187, 188) stout at base, tapering apically to point; upper and lower apical edges serrate; cusp projecting moderately and dentate.

[1] It is impossible to determine which of these two lines represents the posterior thickening of the head capsule until a study of the musculature of the head has been undertaken. This same peculiar feature is found in *Oreopasites,* and there is a suggestion of it in *Neolarra* and possibly also in *Neopasites.*



FIGS. 39–40. Mature larva of *Nomada fowleri* Cockerell. 39. Head, frontal view. 40. Same, lateral view.

FIGS. 41–44. Postdefecating larva of *Nomada* species A. 41. Entire larva, lateral view. 42–44. Left mandible, dorsal, inner, and ventral views.

Scale refers to figure 41.

Maxillae broadly fused with labium; palpi small but rather elongate compared with those of most other nomadine groups. Labium not divided into prementum and postmentum; palpus lost except for single sensillum. Hypopharynx exceeding maxillae and labium, but these three structures all greatly recessed. Salivary opening small, elongate-oval, and surrounded by slightly pigmented, projecting rim.

BODY: General shape (Michener, 1953, fig. 186) of postdefecating form moderately robust, curved, and gradually tapering posteriorly; each body

segment not divided into cephalic and caudal annulets; intrasegmental lines not evident; dorsal tubercles absent; color faintly yellowish. Integument of postdefecating form rigid, non-setose, spiculate ventrally, smooth and shiny. Spiracles (Michener, 1953, fig. 189) small, not on sclerites; atrium projecting above body surface, with rim; atrial wall smooth; peritreme flat; primary tracheal opening with collar. Ninth abdominal segment apparently not protruding ventrally; tenth segment normal in length, not produced ventrally and without spicules.

MATERIAL STUDIED: Two postdefecating larvae, Berkeley, Contra Costa County, California, spring, 1946, from nest of *Andrena complexa* Viereck (J. W. MacSwain), in the collection of the California Insect Survey.

Nomada (*Nomada*) Species A

Figures 41–44

The following description is based on two specimens recovered from a single nest of *Halictus ligatus* Say.[1] Both larvae were allowed to mature, and the adults were examined by Dr. Hugo G. Rodeck who stated (*in litt.*) that the male might be *N. vicina* Cresson and the female may be *N. sayi* Robertson. In view of the fact that they were both taken from the same nest and were identical as larvae, the suggestion is very strong that they actually represent a male and female of the same species.

Total length, approximately 5.0 mm.

HEAD: As described for *N. fowleri* except for following: epipharynx spiculate both laterally and apically; completeness of tentorium not known; otherwise tentorium as in *N. fowleri;* hypostomal and pleurostomal ridges somewhat better defined because of greater pigmentation; pleurostomal-hypostomal angle of head capsule protuberant, much as in *N. suavis.* Mandibular cusp (figs. 42–44) not dentate.

BODY (FIG. 41): As described for *Nomada fowleri,* except spiracles moderate in size.

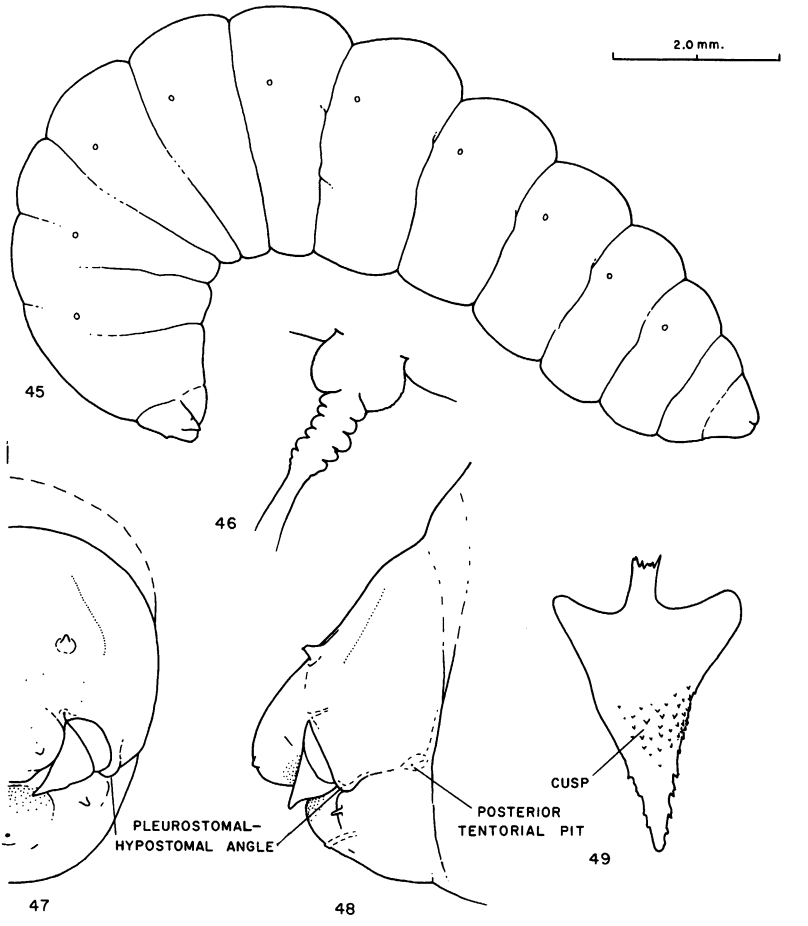
MATERIAL STUDIED: Two postdefecating larvae, Watchung Reservation, Union County, New Jersey; larvae collected from nest of *Halictus ligatus,* August 3, 1964; adults emerged September and October 1, 1964 (A. R. Moldenke), in the collection of the American Museum of Natural History.

Nomada (*Micronomada*) *suavis* Cresson

Figures 45–49

Total length, 8.0 mm.

[1] Identified by C. D. Michener.



FIGS. 45–49. Postdefecating larva of *Nomada suavis* Cresson. 45. Entire larva, lateral view. 46. Spiracle. 47. Head, frontal view. 48. Same, lateral view. 49. Mandible, inner view.

Scale refers to figure 45.

HEAD (FIGS. 47, 48): As described for *N. fowleri* except for following: posterior tentorial pits situated on hypostomal ridge somewhat anterior to posterior thickening of head capsule; epistomal ridge not apparent mesiad of anterior tentorial pits; pleurostomal-hypostomal angle of head capsule somewhat protuberant; antennal papillae more elongate than those of *N. fowleri* and *N.* species A, B, and C; labial palpus somewhat more conspicuous than that of *N. fowleri* and *N.* species A because sur-

rounding area slightly pigmented.

BODY: Shape (fig. 45) as described for *N. fowleri* except for following: spiracles moderate in size; atrial wall (fig. 46) minutely denticulate.

MATERIAL STUDIED: Four postdefecating larvae, Blackfoot, Bingham County, Idaho, August 14, 1947, from nests of *Nomia melandri* Cockerell (G. E. Bohart), in the collection of G. E. Bohart. Identified by G. E. Bohart.

Nomada Species B

Figures 50–53

Total length, 9.0 mm.

HEAD (FIGS. 52, 53): As described for *N. fowleri* except for following: pleurostomal ridge somewhat better defined; pleurostomal-hypostomal angle of head capsule somewhat protuberant. Labral tubercles somewhat larger; mandibular cusp (fig. 51) with fewer teeth.

BODY (FIG. 50): As described for *N. fowleri* except for following: spiracles moderate in size and more heavily pigmented; last pair of spiracles smaller than those of mid-region of body; tenth abdominal segment slightly produced posteroventrally.

MATERIAL STUDIED: Two postdefecating larvae, near Denham Springs, Livingston County, Louisiana, May 8, 1965, from nest of *Andrena flexa* Malloch (E. A. Cross), in the collection of the American Museum of Natural History.

Nomada (*Nomada*) Species C[1]

Figures 54, 55

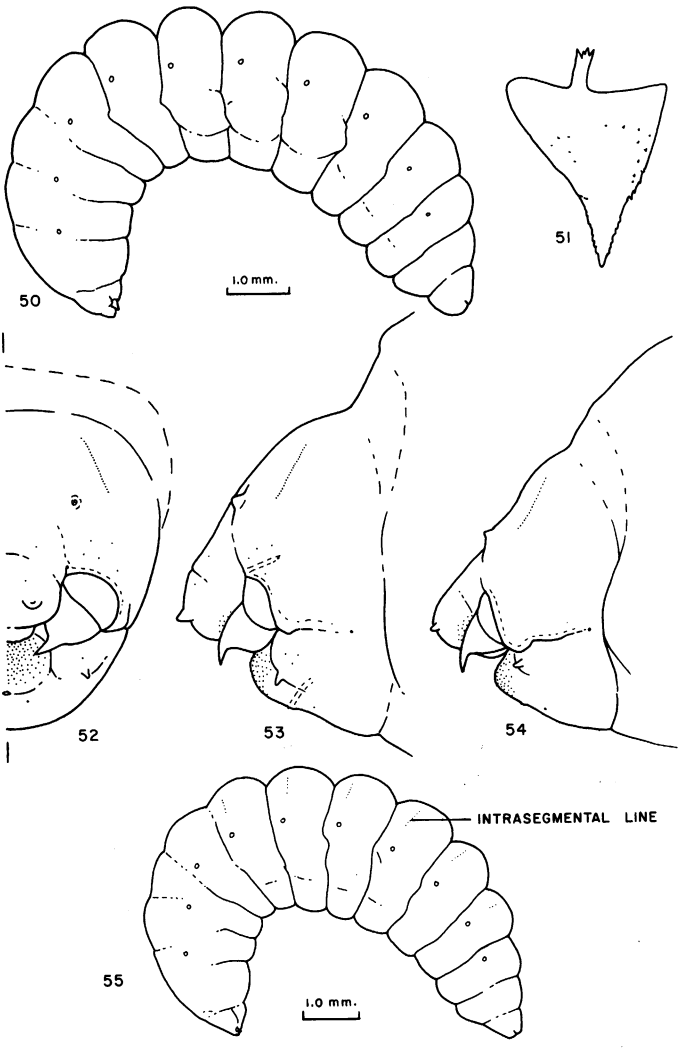
This description is based on two specimens that I am attempting to rear to adulthood. Consequently it is impossible to examine the cleared head capsule in order to provide certain details for the description and illustration. For the same reason, this species is not included in the key, although it will run out to the genus *Nomada.*

Because of the differences between the larvae of *N.* species B and those of species C, the two forms are believed to be separate species.

Total length, 7.5 mm.

HEAD (FIG. 54): As described for *N. fowleri* except for following: spiculation of epipharynx not known; condition of tentorium not known; pleurostomal ridge somewhat better defined; pleurostomal-hypostomal angle of head capsule somewhat protuberant; mandibular cusp apparently dentate but less so than in *N. fowleri.*

[1] After this paper was finished, the adult of this species was identified as to subgenus.



FIGS. 50–53. Postdefecating larva of *Nomada* species B. 50. Entire larva, lateral view. 51. Mandible, inner view. 52. Head, frontal view. 53. Same, lateral view.
FIGS. 54, 55. Postdefecating larva of *Nomada* species C. 54. Head, lateral view. 55. Live larva, lateral view.
Scale refers to figures 50 and 55.

BODY (FIG. 55): As described for *N. fowleri* except for following: faint intrasegmental lines present on some segments; spiracles apparently the same, but subatrium not seen.

MATERIAL STUDIED: Two postdefecating larvae, Alpine, Bergen County, New Jersey, July 7, 1965, from nests of *Andrena bisalicis* Viereck[1] (M. Favreau, O. Hamill, K. Yager), in the collection of the American Museum of Natural History.

TRIBE AMMOBATINI

The larva of a single genus of this small tribe is known.

OREOPASITES COCKERELL

Although the larva of only *O. vanduzeei* is described here, I have collected the immature stages of three other species, some of which are unnamed. These larvae, which will be compared in a forthcoming revision of the genus, appear very similar and agree in at least most respects with the following description.

Oreopasites vanduzeei Cockerell

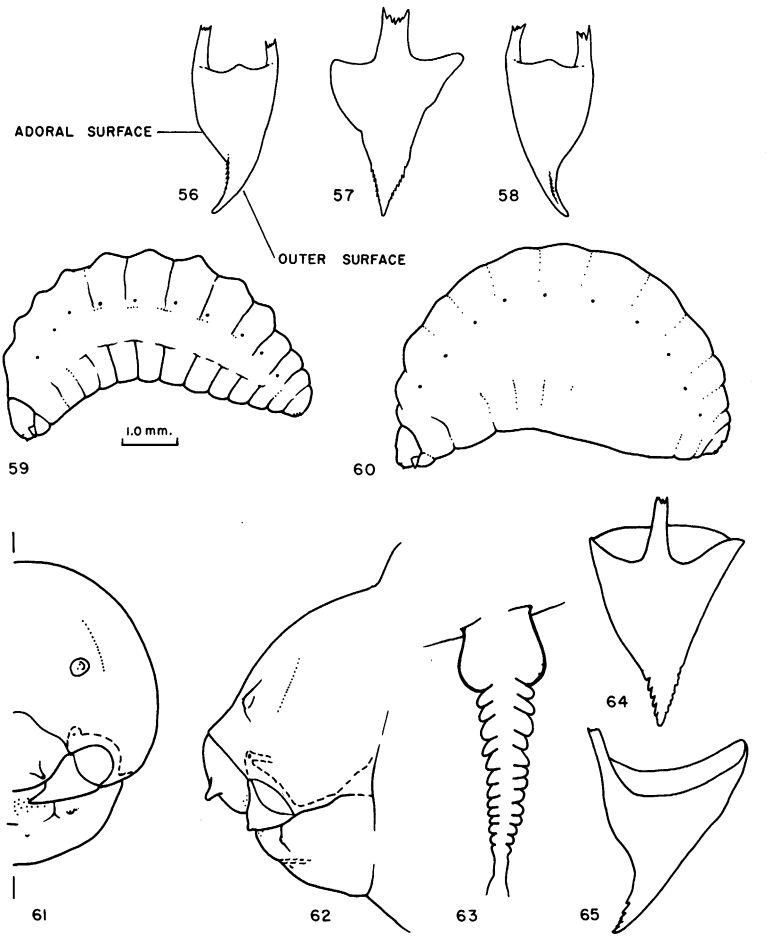
Figures 56–58

The following description is based on some of the same specimens employed in an earlier study (Rozen, 1954).

Total length, 7.0 mm.

HEAD (ROZEN, 1954, FIGS. 5, 6): Integument slightly sclerotized and pigmented; scattered sensilla present; hypopharynx, epipharynx, maxillae, and labium, all non-spiculate. Tentorium incomplete, being represented only by very slender, short, anterior and posterior arms; pits small; posterior tentorial pit situated below ridge and considerably anterior to posterior margin of head; posterior thickening of head capsule virtually obliterated, but head capsule bounded posteriorly by two faint lines, one in front of other, as in *Nomada;* hypostomal ridge moderately well developed and darkly pigmented anterior to posterior tentorial pits; posteriad of pits, ridge becoming narrower until it fades completely at the posterior margin of head; pleurostomal ridge moderately developed and darkly pigmented; epistomal ridge evident laterad of anterior tentorial pits and darkly pigmented; mesiad of pits, ridge on predefecating specimen extending mesodorsally to level of antennae before fading; in postdefecating specimens, ridge scarcely evident mesiad of pits; cleavage line not visible; parietal bands faint. Antennal papillae low, each bearing two sensilla. Labrum moderately projecting and with two moderate-sized tubercles; epipharynx without distinct lobelike swelling above

[1] Associated adults identified by Wallace E. LaBerge.



FIGS. 56–58. Left mandible of mature larva of *Oreopasites vanduzeei* Cockerell, dorsal, inner, and ventral views.

FIGS. 59–65. Mature larva of *Holcopasites insoletus* (Linsley)?. 59. Live postdefecating larva, lateral view. 60. Live predefecating larva, lateral view. 61. Head, frontal view. 62. Same, lateral view. 63. Spiracle. 64, 65. Left mandible, inner and ventral views.

Scale refers to figures 59 and 60.

hypopharynx. Mandible (figs. 56–58) stout at base, tapering apically to point; upper and lower edges serrate; cusp projecting moderately and non-dentate. Maxillae broadly fused with labium; palpi moderate in length, about as in *Nomada*. Labium not divided into prementum and postmentum; palpi lost except for sensilla. Hypopharynx exceeding max-

illae and labium. Salivary opening small, elongate-oval, and not surrounded by low rim.

BODY: General shape of postdefecating form (Rozen, 1954, fig. 1) moderately robust, curved, and gradually tapering posteriorly; each body segment not divided into cephalic and caudal annulets; intrasegmental lines not evident; dorsal tubercles absent, though most body segments of postdefecating form projecting slightly dorsolaterally; color faintly yellowish. Integument of postdefecating form rigid, non-setose, spiculate ventrally, finely wrinkled, and dull. Spiracles (Rozen, 1954, fig. 2) moderately small, not on sclerites; atrium projecting above body surface, with rim; atrial wall with rows of small denticles; peritreme flat; primary tracheal opening with collar. Ninth abdominal segment normal; tenth segment perhaps slightly elongate, not produced ventrally, and without spicules.

MATERIAL STUDIED: One postdefecating larva, one predefecating larva, Tuolumne, Tuolumne County, California, August 3 and June 9, 1953, from nest of *Nomadopsis* (*Macronomadopsis*) *anthidia anthidia* (Fowler) (J. G. Rozen, Jr.), in the collection of the California Insect Survey. Associated adults identified by the author.

TRIBE HOLCOPASITINI

Of the two genera included in this tribe, larvae of only *Holcopasites* are known.

HOLCOPASITES ASHMEAD[1]

The larva described by Michener (1953) as that of *Holcopasites* (under the name of *Neopasites*) is probably a halictid. The following are the first accounts of the immature stages of the genus.

Holcopasites (*Trichopasites*) *insoletus* (Linsley)?

Figures 59–65

The tentative identification of this larva is made on the basis of the numerous *H. insoletus* flying over the nesting site from which the larvae were excavated and on the basis of the large size of the larvae. *Holcopasites* (*Odontopasites*) *arizonicus* (Linsley) and *H.* (*Holcopasites*) *knulli* (Linsley), both smaller than *insoletus,* were also present although most abundant over other nesting areas.

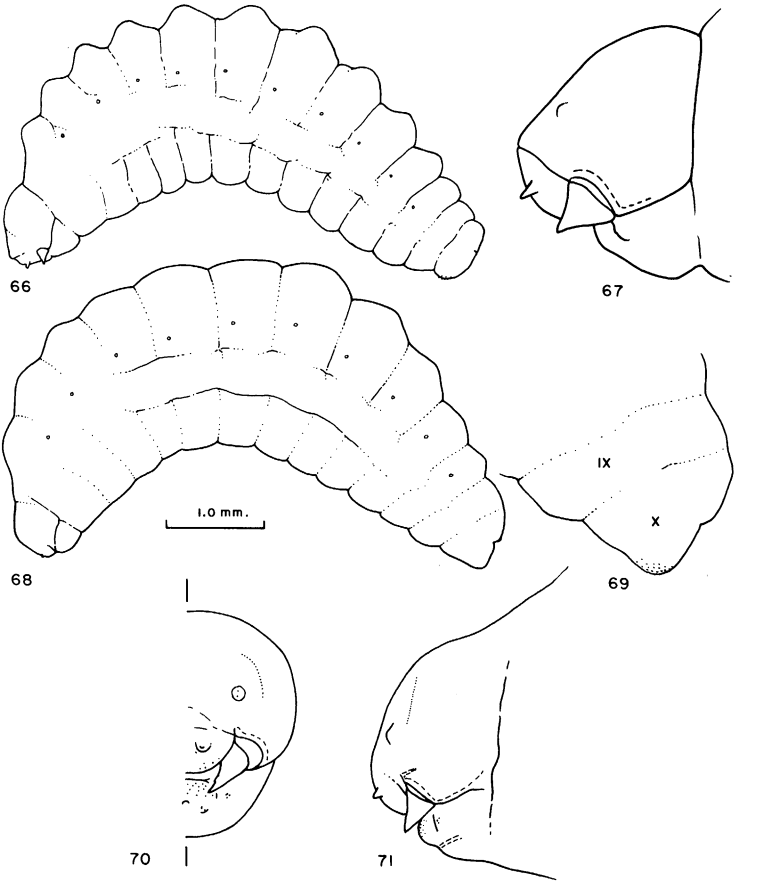
Total length, 5.5 mm.

[1] Associated adults identified by Paul D. Hurd, Jr.

HEAD (FIGS. 61–62): Integument lightly sclerotized and on cleared specimen faintly brownish where thicker; scattered setae apparently entirely lacking; epipharyngeal surface and hypopharynx with scattered spicules; maxillae and labium not spiculate. Anterior tentorial arms thin and short; pits scarcely noticeable on untreated head capsule; posterior tentorial arms and pits absent; posterior thickening of head capsule virtually absent; hypostomal ridge moderately weak anteriorly, less pronounced posteriorly; pleurostomal ridge moderately weak; epistomal ridge weak laterad of anterior tentorial pit and seemingly incorporated with pleurostomal ridge; epistomal ridge obliterated between anterior tentorial pits; cleavage lines not visible; parietal bands faint. Antennal papillae low, each bearing two short sensilla. Labrum a protruding lobe bearing two moderate-sized tubercles; epipharynx without distinct lobe-like swelling basally. Mandible (figs. 64, 65) stout at base but becoming attenuate apically; both upper and lower apical edges moderately finely serrate; cusp not produced and not dentate. Maxillae broadly fused with labium; palpi represented as low convexities, each bearing two or three sensilla. Labium reduced to simple lobe, not divided into prementum and postmentum; palpus lost except for single sensillum on vague swelling. Hypopharynx exceeding maxillae and labium. Salivary opening small, elongate-oval, non-labiate, and without low rim.

BODY: General shape of postdefecating form (fig. 59) robust, slightly curved, and tapering posteriorly; each body segment not visibly divided into cephalic and caudal annulets; distinct dorsal tubercles absent though most body segments of postdefecating form projecting slightly dorsolaterally; mature, predefecating larva extremely robust (fig. 60); color of postdefecating larva yellowish. Integument of postdefecating form rigid, non-setose, finely wrinkled, dull, and non-spiculate except for patches of indistinct spicules situated ventrolaterally immediately behind head. Spiracles (fig. 63) moderately small, not on sclerites; atrium projecting above body wall, with rim, and smooth on inner surface; peritreme flat; primary tracheal opening with collar. Ninth abdominal segment normal; tenth segment normally short, produced ventrally into low, median, slightly pigmented mound; this mound bearing numerous pigmented spicules pointing anteriorly.

MATERIAL STUDIED: One postdefecating larva, one predefecating larva, Southwestern Research Station, near Portal, Cochise County, Arizona, September 8, 1962, from cells of *Pseudopanurgus* (M. Statham), in the collection of the American Museum of Natural History. Rozen (1965b) discussed the biology of this species.



FIGS. 66, 67. Postdefecating larva of *Holcopasites* species A. 66. Live larva, lateral view. 67. Head, lateral view.

FIGS. 68–71. Postdefecating larva of *Holcopasites calliopsidis* (Linsley). 68. Live larva, lateral view. 69. Tip of abdomen, lateral view. 70. Head, frontal view. 71. Same, lateral view.

Scale refers to figures 66 and 68.

Holcopasites Species A

Figures 66, 67

This larva was found in a cell of *Pseudopanurgus* that was near the larvae described above. I believe it to be a different species because of the shape of the head capsule as seen in lateral view and because of the slightly different appearance of the terminal body segment. Its smaller size (4.0 mm.) and thinner aspect may be due to the fact that

it had not consumed its entire food supply, whereas the postdefecating *H. insoletus?* had. In all other major respects it agrees with *H. insoletus?*, although microscopic features such as the sensilla and spiracles were not examined because I had hoped to rear the specimen to adulthood.

Holcopasites (*Holcopasites*) *calliopsidis* (Linsley)

Figures 68–71

Total length, 5.0 mm.

HEAD (FIGS. 70, 71): As described for *H. insoletus?*.

BODY: As described for *H. insoletus?* except form (fig. 68) not so robust; spiracular atrium not projecting above body wall; tenth abdominal segment (fig. 69) more strongly produced ventrally.

MATERIAL STUDIED: Two postdefecating larvae (one of which was reared to adulthood), 11 miles east of Brookville, Jefferson County, Pennsylvania, August 11, 1964 (A. Moldenke); two postdefecating larvae, Watchung Reservation, Union County, New Jersey, August 13, 1964, in nest of *Calliopsis andreniformis* Smith (A. Moldenke); both lots in the collection of the American Museum of Natural History.

TRIBE BIASTINI

The numerous similarities of specialized (i.e., derived) features of the heads of *Neopasites* and *Neolarra* suggest a close relationship between this tribe and the Neolarrini.

The Biastini consist of two genera, *Biastes* and *Neopasites*, neither of which had been collected in the larval stage before.

NEOPASITES ASHMEAD

Neopasites (*Micropasites*) *cressoni* Crawford

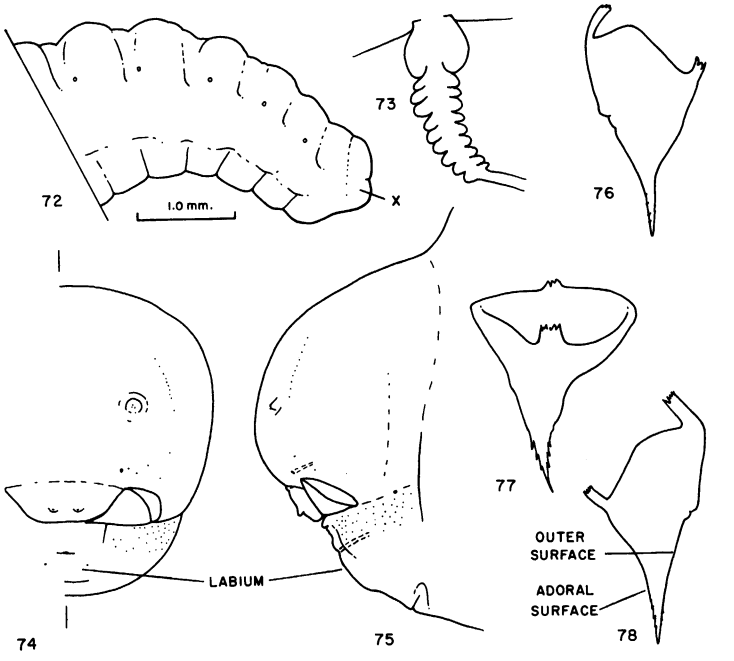
Figures 72–78

Because the larva was badly distorted, the body could not be fully drawn, and certain details of its anatomy are not known.

Total length, 6.0 mm.

HEAD (FIGS. 74, 75): Integument scarcely pigmented, with few scattered sensilla; epipharynx, hypopharynx, and labium without spicules; maxillae spiculate. Tentorium very thin but perhaps complete; anterior pits inconspicuous; posterior pits inconspicuous, on hypostomal ridge anterior to posterior margin of head; posterior thickening of head capsule virtually absent; hypostomal ridge inconspicuous but present; pleurostomal and epistomal ridges absent; cleavage lines absent; parietal bands very faint. Antennal papillae moderately low, each bearing two or three sensilla. Labrum very small, lobelike, exceeded by frontal

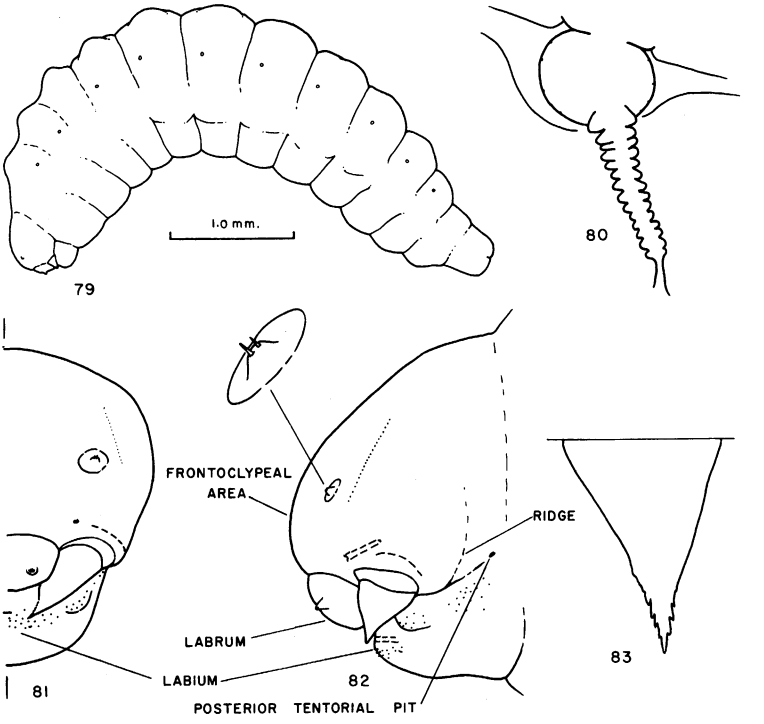
region, and bearing two small but distinct tubercles, all as in *Neolarra;* epipharynx without basal lobelike swelling. Mandible (figs. 76–78) stout at base, tapering to extremely thin point; upper and lower apical edges with few conspicuous sharp-pointed teeth; cusp not projecting; unlike others of Nomadinae except *Neolarra,* adoral surface much shorter than outer surface and mandible straight as seen in dorsal and ventral views.



FIGS. 72–78. Postdefecating larva of *Neopasites cressoni* Crawford. 72. Posterior part of abdomen, lateral view. 73. Spiracle. 74. Head, frontal view. 75. Same, lateral view. 76–78. Left mandible, dorsal, inner, and ventral views.
Scale refers to figure 72.

Maxillae almost indistinguishably fused with labium; palpi discernible only by sensilla. Labium produced slightly more than hypopharynx and maxillae, not divided into prementum and postmentum; palpus lost except for sensillum. Hypopharynx slightly recessed compared to labium and about on line with maxillae; hypopharynx perhaps with transverse projecting area immediately below labrum. Salivary opening small, nonlabiate, and without low rim.

BODY: General shape (fig. 72) of postdefecating larva not fully evaluated because specimen distorted; middle body segments each apparently



FIGS. 79–83. Postdefecating larva of *Neolarra pruinosa* Ashmead. 79. Live larva, lateral view. 80. Spiracle. 81. Head, frontal view. 82. Same, lateral view. 83. Apex of mandible, inner view.
Scale refers to figure 79.

faintly divided into short cephalic annulet and longer caudal annulet[1]; intrasegmental lines faintly evident[1]; dorsal tubercles absent though vague swellings present; color whitish. Integument of postdefecating form rigid, non-setose, spiculate at least ventrally, finely wrinkled, and rather dull. Spiracles (fig. 73) moderately small, not on sclerites; atrium projecting above body wall, without rim; atrial wall smooth; peritreme flat; primary tracheal opening with collar. Ninth abdominal segment either protruding ventrally or with ventral length longer than dorsal so that segment seems to protrude (as in *Neolarra pruinosa*); tenth segment short, not protruding ventrally, and without spicules.

[1] The subdivision of the body segments and the distinctness of the intrasegmental lines may have resulted from the fact that the twisted specimen had to be cleared before it could be examined. These features would not be noticeable on an untreated larva.

MATERIAL STUDIED: One postdefecating larva, Tubac, Santa Cruz County, Arizona, April 16, 1965, from nest of *Dufourea mulleri* (Cockerell) (P. F. Torchio and G. E. Bohart), in the collection of P. F. Torchio and G. E. Bohart. Associated adult determined by the author.

TRIBE NEOLARRINI

The larva of this monogeneric tribe has not been described before. Its marked agreement with *Neopasites* seems to indicate that the Neolarrini and the Biastini are more closely related than we had thought.

NEOLARRA ASHMEAD

Neolarra (Neolarra) pruinosa Ashmead

Figures 79–83

Total length, 4.0 mm.

HEAD (FIGS. 81, 82): Integument lightly sclerotized and but very faintly pigmented; few widely scattered, short setae present; epipharynx and hypopharynx without spicules but labium below salivary opening with scattered spicules; maxillae and labium spiculate. Anterior tentorial arms thin but extending to tentorial bridge; anterior pits inconspicuous; dorsal tentorial arms absent; posterior tentorial arms thin but long so that they meet and bridge foramen; posterior pits evident but inconspicuous; posterior pit anterior to posterior margin of head but relationship to hypostomal ridge not determined because ridge absent[1]; posterior thickening of head capsule virtually absent; hypostomal ridge absent; pleurostomal ridge broad but weak, fading completely anteriorly; epistomal ridge absent; cleavage lines absent; parietal bands very faint. Antennal papillae moderate in size, each bearing two elongate sensilla. Labrum small, lobelike, exceeded by frontal region, and bearing two small but distinct tubercles, which are smaller than those of *Holcopasites* and *Oreopasites;* epipharynx without basal lobelike swelling. Mandible (fig. 83) stout at base, gradually tapering to thin point; upper and lower apical edges moderately finely serrate; cusp neither produced nor dentate; as in *Neopasites cressoni* (fig. 78), adoral surface much shorter than outer surface; mandible slightly curved, not abnormally straight as

[1] On the untreated head capsule, each posterior pit lies in a distinct groove that runs from the posterior mandibular articulation to the pit. Although this groove superficially seems to be the hypostomal sulcus, there is no internal ridge on the cleared specimen to support the idea, and a faint cuticular thickening suggests that the ridge actually lies dorsad of the pit. It would be interesting to learn whether there is a relationship between the posterodorsal extension of this ridge and line A on the head capsules of *Nomada* (fig. 40).

in *Neopasites.* Maxillae very broadly fused with labium; each palpus discernible only by three sensilla. Labium reduced to simple lobe, exceeding both hypopharynx and maxillae; labium not divided into prementum and postmentum; palpus lost except for single sensillum. Hypopharynx exceeded by labium. Salivary opening small, non-labiate, and apparently without low rim.

BODY: General shape of postdefecating larva as figured (fig. 79); each body segment not visibly divided into cephalic and caudal annulets; distinct dorsal tubercles absent, though most body segments of postdefecating larva projecting slightly dorsolaterally; color whitish. Integument rigid, non-setose, minutely spiculate in various places, finely wrinkled, and dull. Spiracles (fig. 80) moderate in size, not on sclerites; atrium projecting above body wall, with rim, and with rows of very fine papillae on inner surface; peritreme apparently having outer rim elevated; primary tracheal opening with collar. Ninth abdominal segment longer ventrally than dorsally so that venter seems to be slightly produced; tenth segment elongate and not produced ventrally or beset with ventral patch of spicules.

MATERIAL STUDIED: Two postdefecating larvae, Fallon, Prairie County, Montana, August 8, 1962, from cells of *Perdita zebrata zebrata* Cresson (J. G. and B. L. Rozen). Associated adults identified by C. D. Michener. Rozen (1965b) has discussed the biology of this species.

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